TAXONOMIC COMMENTS ON THE EURYLAIMIDAE

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INTRODUCTION

The broadbills (Eurylaimidae) are a group of eight genera and 14 species of suboscine passerines confined to the Old World tropics. Newton (1896) credits Baron de Selys-Longchamps with first recognising the eurylaimids as a distinct family in 1842. However, the passerine affinities of the group were not immediately appreciated and in early works it was variously placed near the Caprimulgidae, in or near the Coraciidae, in the Todidae, Muscicapidae, Pipridae or Cotingidae (cf. Sclater 1872). Nitzsch (1867), on the basis of their pterylography, considered the eurylaimids as passerines and put them near the Cotingidae. Sclater (1872), Garrod (1877, 1878) and Forbes (1880a) further established the passerine characteristics of the eurylaimids. To Pycraft (1905) they were osteologically passerine and my own observations confirm that the skeleton in this group agrees well with the basic passerine conformation. In all modern classifications the Eurylaimidae are included in the Passeriformes and there is little doubt that this is their correct ordinal allocation. But their classification within the order is another question altogether.

THE SUPPOSED SUBORDINAL STATUS OF THE EURYLAIMIDAE

The Swedish ornithologist Sundevall (1889) was the first to use the disposition of the deep plantar tendons in birds as a taxonomic character. He found in all the passerines he examined that the tendons of M. flexor hallucis longus and M. flexor digitorum longus were separate for their entire length with no intercommunication via a vinculum as he found in most of the lower orders. Garrod (1877) noted that the broadbills differed from other Passeriformes when he found a vinculum between the deep plantar tendons of three species, and he stated (p. 449) that "The order Passeres falls, therefore, into two sections to start with:—those with the hallux not free, the Eurylaimidae; and those with the hallux independently movable. This latter suborder may again be divided up..." Thus, the first reference to subordinal status for the Eurylaimidae was by inference and no formal names were proposed. This task was left to Garrod's successor, Forbes (1880b), who used the terms Desmodactyli for a suborder containing the Eurylaimidae, and Eleutherodactyli for the remaining passerines. Stejneger (1885) put the broadbills in a superfamily Eurylaimoideae equivalent to Forbes' Desmodactyli. Seebohm (1890) used the term Eurylaemi (amended later to Eurylaimi) for the suborder. This latter terminology and separate subordinal rank for the Eurylaimidae has been adopted by subsequent authors and is the one used in such modern systems of classification as Mayr & Amadon (1951), Wetmore (1960), Sibley (1970), and Ames (1971).

Ridgway (1901), in a key to the suborders of passerines, used four characters to distinguish the Desmodactyli (=Eurylaimi) from the remaining passerine groups. These supposed distinctions were echoed recently by Brodkorb (1968) and most were relied heavily upon by Sibley (1970). I will treat each separately here and make comparisons with the Cotingidae.

DEEP PLANTAR TENDONS

I have already made reference to Garrod's original disclosure of a vinculum between the deep plantar tendons in the Eurylaimidae; specifically in Cymbirhynchus macrorhynchus, Eurylaimus ochromelas, and Calyptomena viridis. It was not until 1914 that Bates
demonstrated that the African genus Smithornis, formerly placed in the Muscicapidae, possesses a deep planter vinculum, thereby giving the first indication that eurylaimids were present outside of Asia. Lowe (1924) confirmed Bates' observations and later (1931) showed that the excessively rare Pseudocalyptomena, of very restricted distribution in Africa, was also a broadbill and had the plantar vinculum present.

I dissected specimens of Eurylaimus javanicus, E. steerei, Serilophus lunatus, Psaromus dalhousiae and Calyptomena whiteheadi, and found a vinculum between the deep plantar tendons in all of them. Bates (1914), in his observations on Smithornis, remarked that the vinculum was weak in all his specimens and may have been absent in one of them. I examined one specimen each of S. capensis and S. rufolateralis and found a narrow, weak vinculum in both. The tendon of M. flexor hallucis longus was not as well developed in this genus as in the other genera of broadbills.

I found no vinculum present in the following species of Cotingidae: Pachyramphus cinnamomeus, Querula purpurata, Cephalopterus ornatus, Gymnoderus foetidus, Procnias nudicollis (3 specimens) and P. tricarunculata. Berger (George & Berger 1966) also found no vinculum in P. nudicollis. Garrod (1877 : 447) reported the lack of a vinculum in Rapicola, although he added the comment that this genus was "thought by some to be intimately related to the Eurylaimidae." The above is a small sample of the large and exceedingly heterogeneous conglomeration of species placed in the Cotingidae and does not preclude the possibility that some species may yet be discovered to have the deep plantar tendons united. Anatomical specimens of some of the more peculiar forms (e.g. Phoenicircus) should be examined for this character as they become available.

What is the taxonomic significance of the deep plantar tendons in this case? Pycraft (1905) disparaged the usefulness of this character in the systematics of the Eurylaimidae. Beddard (1898) calls to our attention that the plantar vinculum is occasionally lacking in Calyptomena viridis. As we have seen, this vinculum is weak and possibly lacking at times in Smithornis. Its presence in any instance, however, may attest to the primitiveness of the broadbills. Because of its occasional absence and because, as I will show below, it is the only distinctive character of the family not known to be shared with some other suboscine group, I do not believe that the presence of a plantar vinculum merits retention of subordinal rank for the Eurylaimidae.

**SPINA EXTERNA OF THE STERNUM**

Sclater (1872) figured the sternum of Cymbirhynchus macrorhynchus (under the name *Eurylaenus javanicus*; cf. Forbes 1880a : 381) and noted that the spina externa (=manubrium) was a simple rod and not forked as in other passerines. The same condition was found in Psaromus (Garrod 1878). Forbes (1880a) reported an unforked spina externa in Eurylaimus ochromelas and Cymbirhynchus, as did Lowe (1931) for Pseudocalyptomena. My own observations showed this condition to obtain in Serilophus lunatus, Calyptomena viridis, C. whiteheadi, and Corydon sumatranus. However, in Smithornis the spina externa is well forked as has been previously reported (Bates 1914, Lowe 1924) and as I can confirm from examination of skeletons of S. capensis and S. sharpei. Lowe (1924) described a slight tendency towards forking in certain specimens of Cymbirhynchus. Despite these reports, subsequent treatments have considered all the broadbills as possessing a simple spina externa (Mayr & Amadon 1951, Wetmore 1960, Brodkorb 1968, Sibley 1970, Ames 1971).

To check further on this character I looked at skeletons of other passerines, especially the cotingas. In the following species of Cotingidae the spina externa was typically forked (nomenclature after Meyer de Schauensee 1966; number of specimens follows the name): Cotinga ridgwayi, 1; C. cayana, 3; Xipholena punicea, 1; Ampelion rubrocristatus, 2; Pipreola rieffleri, 2; P. aureopectus, 1; P. formosa, 1; Attila spadiceus, 1; A. bolivianus, 1; Casiornis rufa, 1; Rhytipterna simplex, 2; R. holerythra, 1; Lipaugus vociferans, 1;
L. unirufus, 1; Pachyramphus rufus, 1; P. homochrous, 1; P. niger, 1; Tityra cayana, 7; T. semifasciata, 11; T. inquisitor, 8; Querula purpurata, 2; Pyroderus scutatus, 1; Cephalopterus ornatus, 4; Perisocephalus tricolor, 1; Gymnoderus foetidus, 2; Rupicola rupicola, 9; R. peruviana, 7. (Of the closely related Pipridae, all the genera I examined had a forked spina externa. These were: Pipra, Antilophia, Chiroxipha, Corapipo, Manacus, Machaeropterus, Neopelma, Tyrannutea, Sapayoa.)

The four species of cotingas in the genus Procnias present a different case. In the two specimens of P. tricarunculata that I examined the spina externa was well forked as in the species above (Fig. 1 (a) and (c)), but in one specimen of P. averano the spina was only slightly notched (Fig. 1 (d)) and two specimens of P. alba and 14 of P. nudicollis varied from very slightly notched to totally simple (Fig. 1 (b) and (e)). So within one genus of cotingas was found the same variation in the spina externa as has been used to define suborders of passerines. The spina externa is also unforked in the Philepittidae (Ames 1971). The forked versus simple spina externa is variable in other orders as well. In the Piciformes either conformation may be found in the Picidae, Capitonidae, Bucerotidae and Galbulidae. The character is also variable in the Coraciiformes and Trogoniformes.

![Figure 1](image-url)

**Figure 1.** Upper: Ventral view of sternum; (a) Procnias tricarunculata showing forked spina externa; (b) P. nudicollis with simple spina externa. Lower: Anterior view of spina externa and carina of sternum; (c) P. tricarunculata (forked); (d) P. averano (slightly notched); (e) P. nudicollis (simple). *s =* spina externa.

Lowe (1924) regarded the taxonomic value of the spina externa as dubious. Since the character is variable within the Eurylaimidae and intragenerically variable in Procnias, it can hardly be of value in maintaining a separate suborder for the eurylaimids. At least in passerines, the unforked spina externa probably represents a primitive condition. If so, the fact that this character is shared by both broadbills and cotingas may be interpreted as demonstrating the relatively primitive nature of these families and supports the possibility that they may be related.

**CERVICAL VERTEBRAE**

The cervical vertebrae, by definition, are those vertebrae anterior to the first vertebra attached by ribs to the sternum. As far as known, all passerines have 14 cervical vertebrae except the eurylaimids, all of which have been thought to have 15. Lowe (1924) in his
discussion of the anatomy of *Smithornis* does not mention the number of cervicals, although he notes (1931) that *Pseudocalyptomena* has 15. In two specimens of *Smithornis capensis* and two of *S. sharpei* I found that there were only 14 cervical vertebrae, the typical passerine condition. Actually this difference in the number of cervicals does not represent a decrease in the total number of vertebrae but rather the acquisition of a single pair of sternal ribs, thus converting what was the posteriormost cervical vertebrae into the anteriormost thoracic vertebrae. The number of cervical vertebrae cannot be used to distinguish the Eurylaimidae from other passerines, even on the familial level, much less subordinally. That most species have 15 again reflects the primitiveness of the eurylaimids.

**HALLUX**

Ridgway (1901 : 14), in his key to the suborders of Passeriformes, gives as a distinguishing character of the Desmodactylidi (=Eurylaimi), "hallux weak" as opposed to "hallux strongest toe" in the Eleutherodactylidi. This is repeated by Brodkorb (1968) in his diagnosis of the subgroupings of passerines. The basis for making this distinction is not at all clear to me and it would seem to be a very subjective one at best. I have examined specimens of all the species of broadbills and cannot detect any consistent difference between their halluces and those, for instance, of most cotingas. "As regards position, structure and size, the hallux is the most variable of all the toes, and its taxonomic value is very limited" (Newton 1896 : 404). It is not a sound basis for attributing subordinal rank to any group even if a difference were detectable.

**QUADRATO-JUGAL ARTICULATION**

The following statement by Lowe (1931 : 460) implies that the quadrato-jugal articulation of the Eurylaimidae is distinctive: "In the Eurylaemids the quadrato-jugal makes junction with the outwardly projecting spur at the lower end of the quadrate by means of what is nearly a symphysis; whereas in such forms as the crows, starlings, etc. there is a cup-and-ball joint." No mention is made of other subosine forms, however. In a quick survey of skeletons, I found the "eurylaimid-type" articulation in the Cotingidae, Pipridae, Tyrannidae, Phytotomidae, Rhinocryptidae, Furnariidae, Dendrocoptilidae, Formicariidae and Ptilidae (I was not able to examine skeletons of the Acanthisittidae or Philepittidae), and a ball-and-socket articulation in the Menuridae and all oscine families examined. This is an interesting character, worthy of further study, and may provide a demarcation between oscines and suboscines; but it cannot be used to distinguish the broadbills from other oscines.

To recapitulate, all the characteristics that have been used to isolate the Eurylaimidae from the remaining subosine passerines in a suborder of their own have been shown to be variable intrafamilially or shared with other families. I therefore recommend that the subordinal designation "Eurylaimi" be abandoned and that the Eurylaimidae be included in the suborder Tyranni.

**THE RELATIONSHIPS OF THE EURYLAIMIDAE**

Sclater (1872 : 179) long ago stated: "I believe, however, that Mr Wallace [1856] will probably be found to be correct in considering the Eurylaimidae the paleogen representatives of the neotropical Cotingidae." Stejneger (1885) was of the same persuasion. Sundevall (1889 : 130) felt that the Eurylaimidae were "scarcely to be distinguished from the American ones [of his Rupicolinae, which included *Lamisoma, Phoenicircus*, and *Rupicola*] in any general way." Ridgway (1901 : 15), in speaking of the eurylaimids, said that they were a small group "confined to the Indo-Malayan region [the African species were not known to be eurylaimids at the time], where it takes the
place of the rather closely related haplophone Clamatores (especially the family Coti-
gidae) of the Neotropical region." Shortly after this, Pyrcraft (1905) published his paper
on the osteology of the Eurylaimidae wherein he was much impressed with the resemblance
of the skeletons of eurylaimids and cotidgas. He repeatedly emphasised the similarity
of the skulls of Calyptomena and "Chasmorhynchus" (=Procnias)*, especially of the
lacrimaliyjs, premaxillaries, and maxillicpalatine processes. These shared skeletal characters
and resemblances of the musculature, syrinx, and pterylography led him so far as to say
that "It is quite possible that further investigation will show that the Eurylaimidae are
entitled to rank no higher than a subfamily of the Cotingidae " (p. 55). Later (1907), he
recognised four suborders of passerines and included the Cotingidae, Pipridae, and
Phileiptitidae along with the Eurylaimidae in his suborder Eurylaimi. For some reason,
these opinions have been ignored or overlooked by subsequent authors who have preferred
to recognise the differences that were perhaps overemphasised by Garrod and Forbes.

There are other points of similarity between the broadbills and cotidgas. The great
width of the bill that gives rise to the vernacular name of the Eurylaimidae (and which
reaches the extreme for passerines in Corydon) is not found throughout the family. The
three species of Calyptomena possess bills of normal passerine proportions. In Fig. 2
the skull of C. viridis is contrasted with Procnias nudicollis and it can be seen that not only
is there little difference in bill proportions, but also the overall likeness of the skulls is
apparent, as Pyrcraft noted. The similarity of the tuft of feathers that cloaks the bill of
Calyptomena to the crown of Rupicola, which also envelopes the bill, while perhaps not
significant, is certainly suggestive.

FIGURE 2. Dorsal view of skull: (a) Procnias nudicollis; (b) Calyptomena viridis.

Broadbills are uniformly described as building large, bulky, pendant nests with an
opening on the side. While the nesting habits of cotidgas are exceedingly diverse
(cf. Skutch 1969) the nests built by Pachyramphus and Platysaris are strikingly like
those of eurylaimids. Little seems to be known about the ethology of broadbills but
Bates (1914) has described behaviour of Smithornis and Chapin (1953) has described
display behaviour in Smithornis Rufolateralis. Males of this genus perform a darting
circular flight while emitting a croaking noise that is believed to be made by the wings.
This whole procedure is reminiscent of certain of the Pipridae, a family intimately
related to the cotidgas, and some species of which perform similar displays using the
wings most effectively as organs of sound production. Both the Eurylaimidae and
Cotingidae contain strikingly coloured species clothed in various shades of green, violet,

*I should point out here that Sibley (1970: 36) is entirely in error in making the statement that
Lucas "recommended the establishment of a separate family, the Procniiad, for the bellbirds
based upon palatal characters. Lucas" (1895) paper concerns the Swallow-tanager Terina viridis
and no mention is made of bellbirds. Procnias and Procniad were synonyms for Terina and
Tersinidae, respectively, that were in use in Lucas' time.
red and yellow. Both families consist of insectivorous and frugivorous birds of the treetops and do not seem to have evolved terrestrial or creeping forms. Certain members of both families have concealed white patches in the shoulder area that are revealed at times in displays, e.g. *Smithornis* (Bates 1914) and *Platycercus* (Skutch 1969).

Sibley (1970) has presented a detailed review of the taxonomy of the Passeriformes, including his new information derived from egg-white protein analyses. Of the Eurylaimidae he says (p. 33), "The broadbill [egg-white protein electrophoretic] patterns resemble those of the cotingas (*Platycercus*) and tyrannids but not any more closely than those of several other groups." And he continues—"...because of ample anatomical evidence to the contrary the resemblances to the New World groups cannot be considered important". However, I think that I have shown that such ample contrary evidence is not available and therefore the egg-white protein data can at least be regarded as not contradicting a relationship between the eurylaimids and the New World suboscines, if not actually supporting such a view. I agree with Sibley that the broadbills are not closely related to the Pittidae, Mackworth-Praed (1964) and others to the contrary. Sibley gives evidence that neither the Pittidae nor Acanthisittidae are closely related to the other suboscine families and suggests an as alternative that they may be derivatives of oscines. But as I have mentioned, the quadrate-jugal articulation, at least in *Pitta*, is typically suboscine.

From their present distribution the eurylaimids evidently represent a scattered remnant of rather specialised species from an ancient passerine lineage of once wider distribution. There are eight genera, five of which are monotypic. None of these genera seems to me to be particularly closely related to any of the others. In Africa, where there are only two genera, even these two are not at all closely related. *Pseudocalyptomena graminea* is found only in a small area of forest in the Congo and Uganda (Friedmann 1970). *Calyptomena hostei* and *C. whiteheadi* are restricted to a few mountain-tops in Borneo. *Eurylaimus steerii*, found only in the Philippines, was once put in a separate genus (*Sarcophanops*) and is quite distinct from the other two species of *Eurylaimus*. Ballman (1969) reports a fossil eurylaimid of undetermined relationships from Lower Miocene deposits in Bavaria. All this suggests that the family is a retreating one. Modern eurylaimids probably represent the oldest remaining passerine stock. Their ancestors very likely arose in the Old World tropics early in the Tertiary and distributed themselves widely throughout the world in suitable habitat. With the rise of the more advanced oscines (also probably in the Old World tropics) at some later point in the Tertiary, this ancestral suboscine stock would have been largely replaced everywhere except in South America, which was isolated through the Tertiary until the end of the Pliocene. This isolation allowed for the persistence and radiation of the suboscines that characterise the South American passerine fauna today, in comparative freedom from the oscine onslaught taking place in the rest of the world. Only a few specialised remnants of this original primitive passerine stock survived the takeover in the Old World, these being the existing Eurylaimidae. This is consistent with a general picture of animal distribution presented by Darlington (1957) wherein many vertebrate groups appear to have arisen in the Old World tropics and a number of groups became isolated and diversified in South America. (After writing the above, I find that Amadon (1957) has proposed a nearly identical theoretical history of the suboscines.)

To get an impression of how diverse the genera of eurylaimids probably are, let us imagine widespread replacement and extinction among the Cotingidae. Suppose we were left with only the eight genera *Phialura, Querula, Conioptilon, Iodopleura, Cephalopterus, Procias, Phoenicircus*, and *Xiphonema*; an exceedingly heterogeneous group of species. It is quite conceivable that taxonomists might have separated such an assemblage into a number of subfamilies or even families (as some do now for *Rupicola*). Such a vast extinction probably took place among the Eurylaimidae, leaving a hodgepodge of more or
### Table 1
Recent classifications of the suboscine passerines with a suggested rearrangement

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less unrelated genera. For this reason I do not think that it is useful to maintain a separate subfamily of the Eurylaimidae for Calyptomena (Calyptomeninae) as was done by Sclater (1888) and subsequently by Ames (1971). Smithornis, for instance, is at least as divergent as Calyptomena. It is appropriate here to bring up another point concerning Smithornis. This genus was listed first by Peters (1951) in his treatment of the Eurylaimidae, thereby presumably indicating it to be the most primitive of the family. What his reasoning was for this I do not know; perhaps he was influenced by the rather plain colours of Smithornis as compared to the rest of the broadbills, although Amadon (1957) suggests that subdued colour may be an advanced character in passerines. However, by virtue of possessing a weak plantar vinculum, a forked spina externa, and 14 cervical vertebrae, Smithornis certainly may be considered to be the most advanced genus in its family and therefore should be placed at the end of any listing of the Eurylaimidae.

THE SEQUENCE OF SUBOSCINE FAMILIES

We may now discuss some aspects of the phylogeny of the entire group of suboscines. For this purpose, I have included a list (Table 1) with two of the most widely followed systems of classification to which I have appended a suggested rearrangement. The higher categories of passerines have usually been defined on the basis of the structure of the syrinx. To previous studies we may now add the monumental work of Ames (1971) who has greatly augmented and clarified our understanding of this subject.

In the Eurylaimidae, the syrinx is very simple and unspecialised, a condition once again indicating the primitiveness of the family. But this structure is not sufficiently distinct from that of certain other suboscines, especially some of the cotingas, to differentiate the broadbills from them. For these reasons as well as those given previously, I place the Eurylaimidae at the beginning of the suborder Tyranni.

The syrinx in the Philoptilidae is very similar to that of the Eurylaimidae and the family also possesses an unforked spina externa. These birds probably represent a specialised offshoot of the ancestral Old World suboscine lineage, long isolated on the ancient Madagascar land-mass. I place them therefore, after the Eurylaimidae.

The Pitiidae and Acantihnatiidae do not as yet present any obvious affinities to other passerine families but it does seem fairly certain that they do not belong with the distinctive and relatively homogeneous oscine group. In our present state of knowledge they are best treated as Tyranni incertae sedis as I have done here, meaning to imply no relationships by their terminal position.

The remaining suboscine families have been divided into two groups, usually at the superfamily level. In the Tyrannidae the syrinx is exceedingly variable, some forms being quite primitive. In the Furnariidae the syrinx, although more variable than in the oscines, presents elaborate and specialised structures that are shared by all the families of the group and that are found in no other passerines. For this reason and because there are no characters to ally them particularly to the Tyranni," Ames (p. 153) elevates the Furnariidae to the rank of suborder. What may be said of their relationships, however, is that they are not oscines. While it is possible that such a negative approach to classification may have drawbacks, I prefer to retain the Furnariidae as a superfamily within the suborder Tyranni. It appears likely that this group has been derived from the more primitive suboscine types in South America and that in their specialisation of the syrinx and subdued colours they have somewhat paralleled the development of the oscines. Assuming the Furnariidae to be more advanced, I place them after the Tyrannidae, a position in which, strangely, they have not appeared in any recent classification although they may be found there in the lists of Stejneger (1885), Sharp (1911) and others. Within the Furnariidae, as within the Tyrannidae, family limits are often difficult to discern. The relationships of the Furnariidae and Dendrocolaptidae may be more complicated than is reflected by most treatments (cf. Sibley 1970 : 33) but as currently conceived, the Dendrocolaptidae with their more specialised habits and syringes should probably be placed after the Furnariidae. I follow Ames et al. (1968) in relegating the two genera of the Coropophagidae to the Formicariidae and Tyrannidae.

The Tyrannidae, the Cotingidae contain the most primitive Neotropical forms. With the Pipridae and Phaethoniidae they form a fairly close group (Sibley; Ames) followed by the diverse Tyrannidae. As has been pointed out, the family limits here are by no means always clear.

The Menuridae of Australia are an anomalous group well deserving of their subordinal status. While their relationships remain uncertain, it is my present opinion that they will ultimately be found to be closer to the Oscines than the Tyranni.

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SUMMARY

On the basis of supposed differences in the shape of the spina externa of the sternum, the number of cervical vertebrae, the deep plantar tendons, the quadrate-jugal articulation, and the size of the hallux, the Eurylaimidae were put in a separate suborder, the Eurylaimi. All of these characters are now shown to be variable within the family or shared with other suboscine families. It is recommended that the subordinal designation "Eurylaimi" be abandoned and that the family be included in the suborder Tyranni. A number of characters point to the Cotingidae as the nearest possible extant relatives of the Eurylaimidae. The Eurylaimidae consist of a number of unrelated genera with several relict species, and probably represent the remains of an ancient, once more widespread group that became isolated and gave rise to the suboscine faunas in South America while being largely replaced by oscines in the Old World. Recognition of subfamilies within the Eurylaimidae is discouraging. Smithornis should be considered the most advanced of the eurylaimids. The sequence of suboscine families is discussed and a rearrangement is suggested.

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